

Pollution control can help mitigate future climate change impact on European grayling in the UK

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Abstract

Aim: We compare the performance of habitat suitability models using climate data only or climate data together with water chemistry, land cover and predation pressure data to model the distribution of European grayling (*Thymallus thymallus*). From these models, we (a) investigate the relationship between habitat suitability and genetic diversity; (b) project the distribution of grayling under future climate change; and (c) model the effects of habitat mitigation on future distributions.

Location: United Kingdom.

Methods: Maxent species distribution modelling was implemented using a Simple model (only climate parameters) or a Full model (climate, water chemistry, land use and predation pressure parameters). Areas of high and low habitat suitability were designated. Associations between habitat suitability and genetic diversity for both neutral and adaptive markers were examined. Distribution under minimal and maximal future climate change scenarios was modelled for 2050, incorporating projections of future flow scenarios obtained from the Centre for Ecology and Hydrology. To examine potential mitigation effects within habitats, models were run with manipulation of orthophosphate, nitrite and copper concentrations.

Results: We mapped suitable habitat for grayling in the present and the future. The Full model achieved substantially higher discriminative power than the Simple model. For low suitability habitat, higher levels of inbreeding were observed for adaptive, but not neutral, loci. Future projections predict a significant contraction of highly suitable areas. Under habitat mitigation, modelling suggests that recovery of suitable habitat of up to 10% is possible.

Main conclusions: Extending the climate-only model improves estimates of habitat suitability. Significantly higher inbreeding coefficients were found at immune genes, but not neutral markers in low suitability habitat, indicating a possible impact of environmental stress on evolutionary potential. The potential for habitat mitigation to alleviate distributional changes under future climate change is demonstrated, and specific recommendations are made for habitat recovery on a regional basis.

KEYWORDS

climate change, conservation, European grayling, habitat improvement, pollution, species distribution modelling

1 | INTRODUCTION

Human ecosystem alteration, such as habitat loss and degradation, invasive species and overharvesting, can cause environmental stress (Brown, Saunders, Possingham, & Richardson, 2013; Crain, Kroeker, & Halpern, 2008), which can directly impair the adaptive potential of populations and increase vulnerability to extinction (Charmantier & Garant, 2005; Frankham, 2005; Hoffmann & Hercus, 2000). These stressors are thought to be impacting biodiversity in a way comparable to historic mass extinction events (Ceballos et al., 2015) with unprecedented declines in global biodiversity now occurring.

These impacts on biodiversity are now exacerbated by climate change through cumulative or synergistic effects (Brook, Sodhi, & Bradshaw, 2008). Climate change is expected to become a major threat to biodiversity over the next decades (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Thomas et al., 2004), and the integration of climate change predictions into current conservation and biodiversity planning is therefore essential (Araújo, Cabeza, Thuiller, Hannah, & Williams, 2004; Heller & Zavaleta, 2009). Such integration requires knowledge of the sensitivities of species to various climatic parameters in order to assess vulnerability to climate change (Hulme, 2005). A synergistic approach incorporating habitat change and degradation with exposure and sensitivity to climate change and adaptive capacity will further improve vulnerability analysis (Dawson, Jackson, House, Prentice, & Mace, 2011; Williams, Shoo, Isaac, Hoffmann, & Langham, 2008). The investigation of differences in habitat quality may serve as a predictive framework to assess evolutionary potential across the range of a species because there is a close relationship between environmental conditions and genetic diversity (Charmantier & Garant, 2005; Frankham, 2005; Hoffmann & Hercus, 2000).

Species distribution modelling (SDM) can be used to identify key environmental parameters that affect the distribution of a species, by combining species occurrence with environmental data (Elith & Leathwick, 2009). These models are powerful tools to assess specific sensitivity to environmental change and to predict the influence of climate on species distribution (Thomas et al., 2004). The implementation of SDMs has been successful in conservation and reserve planning (Rodríguez, Brotons, Bustamante, & Seoane, 2007), invasive species management (Jiménez-Valverde et al., 2011), epidemiology research (Puschendorf et al., 2009) and predicting potential effects of climate change on biodiversity (Hijmans & Graham, 2006).

The classical approach of SDMs is to model "bioclimatic envelopes" (Pearson & Dawson, 2003) because climate is usually the dominant factor in determining species ranges (Araújo & Peterson, 2012) and climatic variables are therefore considered sufficient to describe changes in distribution (Bucklin et al., 2015). As a first approximation, this approach can describe or predict niche requirements and

indicate where tolerance limits are exceeded under conditions of climate change (Pearson & Dawson, 2003). However, improvements in model performance can be made by the addition of non-climate parameters, particularly at small spatial scales, where other local factors can become dominant (Pearson & Dawson, 2003; Pearson, Dawson, & Liu, 2004; Stanton, Pearson, Horning, Ersts, & Reşit Akçakaya, 2012). This approach allows development of climate change mitigation strategies through the identification of non-climate-related drivers of biodiversity change (Pereira et al., 2010). Sutton and Soto (2012) show that predictive performance is highest when there are interactions between climatic and other variables. These authors highlight the importance of including variables such as land cover to study their effect in combination with climate (Stanton et al., 2012).

European grayling (Salmonidae, *Thymallus thymallus*) is a protected species (listed in appendix III of the Bern convention) of conservation and economic importance (Swatdipong, Primmer, & Vasemägi, 2010), that, even in comparison with other salmonids, shows high sensitivity to high temperature (Ibbotson et al., 2001; Jonsson & Jonsson, 2009) and exhibits narrow water quality requirements (Oberdorff, Pont, Hugueny, & Porcher, 2002; Uiblein, Jagsch, Honsig-Erlenburg, & Weiss, 2001). As such, grayling make an ideal indicator species of habitat quality and climate change. We aim to investigate the influence of climate and other habitat quality parameters on the distribution of this species. Specifically, we (a) compare a Simple climate-only model with one that incorporates the sensitivity of grayling to habitat quality parameters (i.e. current velocity, land use, water chemistry and predator density); (b) test associations of habitat quality and neutral and adaptive genetic diversity; (c) forecast grayling distributions under future climate change scenarios; and (d) investigate the effects of habitat improvement on future distributions. The results are discussed in the context of conservation management.

2 | METHODS

2.1 | "Simple" versus "Full" model

For our climate-only model, data across the latitudinal range of grayling were used to identify relevant bioclimatic parameters (Figure 1, right panel; see Results Table 1). The eastern part of the longitudinal range of European grayling (adjacent to the Ural Mountains) was omitted to avoid bias due to low numbers of records available in that area. Subsequently, we focussed on a subset study area (Figure 1, left panel), representing the distribution of European grayling in England and Wales. This area was chosen because it is represented by multiple, extensive data sets on water quality parameters obtained from long-term surveys conducted by the UK Environment Agency and

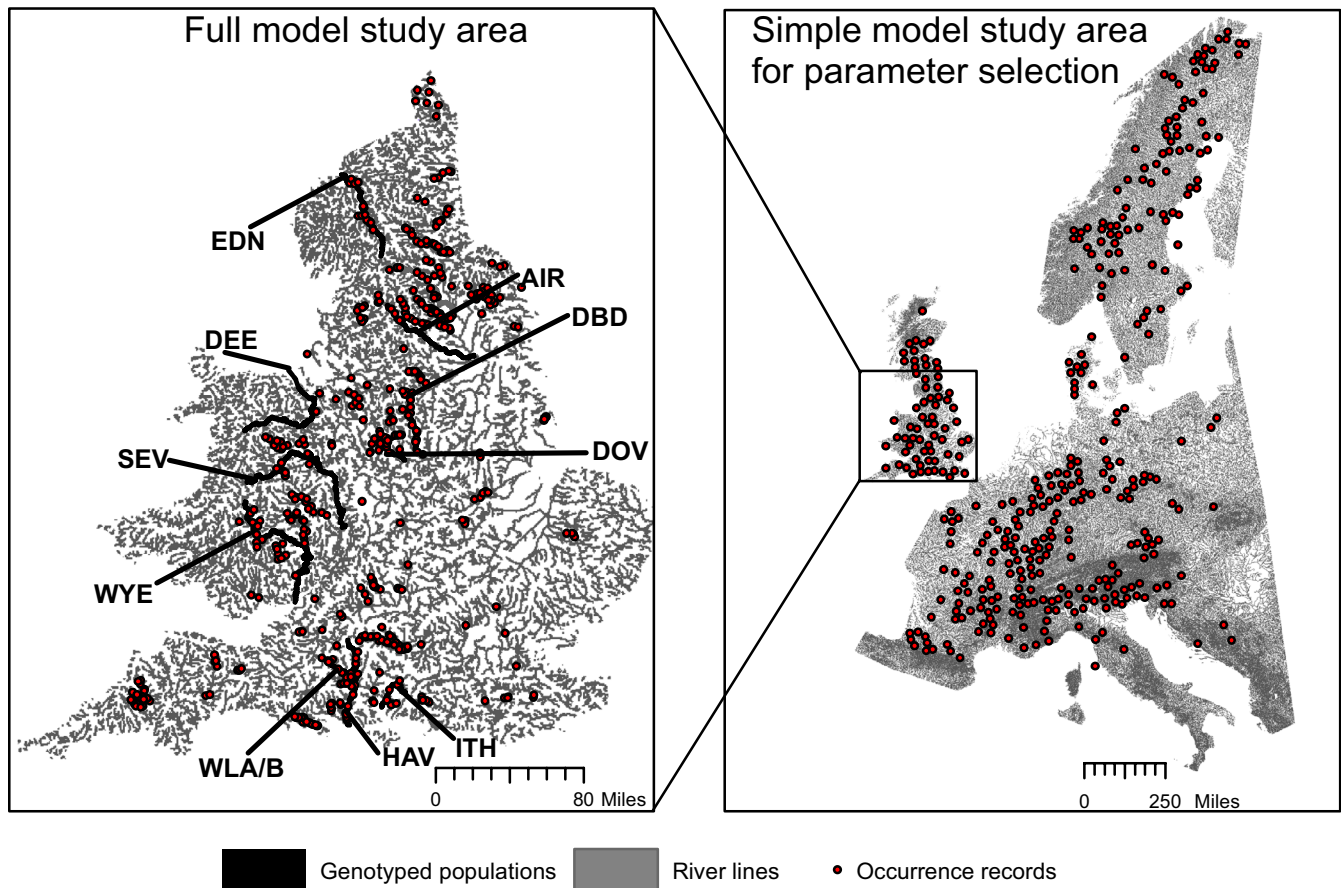


FIGURE 1 Right: Study area used for the selection of bioclimatic variables; Left: Subset study area; unique occurrence records of *Thymallus thymallus* are shown in red; these were spatially rarefied at a scale of 30 km² for the entire European distribution (right) and at a scale of 1 km² for the subset study area (left); populations genotyped at microsatellite and MH loci are shown in black, river lines are shown in grey

direct measurements of river surface water temperature (Orr et al., 2010). These data sets were used in the Full model with the aim to assess the sensitivity of grayling to non-climatic parameters that impact on habitat suitability. The same subset study area was used in the Simple model to allow for comparison of model performance when using only climate data.

2.2 | Development of the Full model

Unique occurrence points (2,846) recorded since 1990 for European grayling were obtained from the GBIF database in 2014 (www.gbif.org) (Figure 1). This time frame was selected as there is a lack of recently updated records in GBIF, so that only using records made after 2000 would significantly underestimate the current distribution. To account for uneven sampling effort and to reduce spatial clustering, subsampling of occurrence records was done using the SDM toolbox (Brown, 2014) for ArcGIS 10.3 (ESRI). Records were spatially rarefied at a scale of 30 km² across the latitudinal range, which minimized a biased distribution of records, due to differences in sampling efforts across different countries, leaving 292 records in total (Figure 1, right panel). For the final subset study area, records were rarefied

at a scale of 1 km², leaving 441 records in total (Figure 1, left panel). The scale is the same as the resolution of environmental layers and was chosen due to the generally high site fidelity of grayling, aiming for a maximal resolution of small-scale differences in habitat preference (Nykänen, Huusko, & Lahti, 2004). Only occurrence points that had records for all environmental parameters were used for model tuning and evaluation. There were 441 occurrence points for the Simple model and 283 for the Full model.

A number of predictive variables were selected based on the biology of European grayling and data availability. Bioclimatic parameters were selected (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) based on their relative importance in explaining the entire latitudinal distribution of grayling from a preliminary model (Figure 1, right panel; Table 1). Land cover data for the year 2000 were retrieved from the European Environmental Agency at a resolution of 100 m. Predation by the great cormorant (*Phalacrocorax carbo*, hereafter cormorant) on inland fish populations has increased significantly over the past thirty years (Callaghan, Kirby, Bell, & Spray, 1998), having severe local impact in some cases (Vetemaa et al., 2010). To investigate the impact of this predator, GBIF records of cormorant since 1990 were used to estimate spatial patterns of abundance using a Gaussian kernel density

TABLE 1 Initial variable set used in the variable selection process of the Full model; Bioclimatic variables considered are those that were selected across the European distribution of grayling

| Climate | Human habitat modification | | | Biotic interactions | |
|---|----------------------------|-----------------|------------------------|--------------------------------|---|
| Bioclimatic variables (WorldClim) | Water temperature | Flow | Land use | Water chemistry | Predation |
| Isothermality (Bio 2/ Bio 7) (* 100) (Bio 3) | Autumn Mean | Flow average | Land cover 2000 | Biological Oxygen Demand (BOD) | <i>Phalacrocorax carbo</i> density |
| Temperature seasonality (standard deviation *100) (Bio 4) | Spring Mean | Flow Q10 | | Calcium | |
| Max temperature of warmest month (Bio 5) | Summer Mean | Flow Q95 | | Chloride | |
| Min temperature of coldest month (Bio 6) | Winter Mean | | | Copper | |
| Mean temperature of wettest quarter (Bio 8) | | | | Nitrate | |
| Mean temperature of driest quarter (Bio 9) | | | | Nitrite | |
| Mean temperature of coldest quarter (Bio 11) | | | | Orthophosphates | |
| Precipitation of driest month (Bio 14) | | | | Ph | |
| Precipitation seasonality (coefficient of variation) (Bio 15) | | | | Suspended solids | |
| Precipitation of wettest quarter (Bio 16) | | | | Total ammonium | |
| Precipitation of warmest quarter (Bio 18) | | | | | |

Note: Parameters retained in the Full model are shown in bold.

function, which smooths individual occurrence counts per grid cell (Silverman, 2018), which was 10 km² here, using the SDM toolbox (Brown, 2014) for ArcGIS 10.3 (ESRI). As this estimate of density may be biased and confounded by sampling intensity, we additionally generated a categorical presence/absence layer based on the observation of occurrence records within a 10-km² grid cell and compared model predictions. Measurement of biochemical oxygen demand (BOD), concentration of calcium, chloride, copper, nitrate, nitrite and orthophosphates, pH, suspended solids and total ammonium were obtained from long-term surveys conducted by the UK Environment Agency. As it is necessary to acquire data from a large number of occurrence and background points, a good spatial coverage of measurements was ensured (minimum of 6,000 sites) after filtering using the following approach. To remove outliers for each site, all records since the year 2000 were averaged for the variables above and sites were removed if either the mean or the standard deviation exceeded a modified z-score of 3.5 (Iglewicz & Hoaglin, 1993). Water temperature measurements were derived from the River Surface Water temperature database as described in Orr et al. (2010). For each region, all records since 1985 were extracted and were again filtered if measurements exceeded a modified z-score of 3.5. Of the remaining records, averages were calculated per site, separately for each season. The time period was chosen to maximize the records per site in order to resolve local differences despite strong fluctuations. River flow data were obtained from the Future Flows and Groundwater Levels data set (Prudhomme et al., 2013; Haxton et al., 2012), specifically the national maps of changes in river flow statistics (Prudhomme, 2012). Current flow data were based on observed rainfall and potential evapotranspiration input from 1961 to 1990 (more details in Prudhomme, 2012). Mean annual flow rate and the 5th (Q95) and

90th (Q10) percentile of the annual flow rate were used, which are commonly chosen to represent flow regimes (Dunbar et al., 2010). The Q95 flow value is exceeded 95% of the time and represents low flow, while the Q10 flow value is exceeded 10% of the time and reflects high flow. We investigated the effect of extreme levels of flow here apart from the annual average, as these have been suggested to be of particular importance for the survival of juvenile salmonids (Riley, Maxwell, Pawson, & Ives, 2009; Warren, Dunbar, & Smith, 2015). For all point measurements, a buffer of 2km was created and raster layers were created at a resolution of 30" (0.93 × 0.93 = 0.86 km² at the equator), assigning the value closest to the centre of the cell using ArcGIS 10.3 (ESRI). All layers were projected in ETRS 1989. Table 1 lists variables tested for relative impact on habitat suitability for grayling.

2.3 | Variable selection, model calibration and evaluation

We used model selection to avoid overfitting the data. Briefly, we used a stepwise variable selection process including species-specific tuning of regularization and AICc as an evaluation metric (see Warren, Wright, Seifert, & Shaffer, 2014; Zeng, Low, & Yeo, 2016). During the variable selection process, all considered parameters were iteratively added to the model in order of their contribution to an initial evaluation model and only retained if their addition resulted in a reduced AICc compared to their omission. While this method does not directly control for collinearity among predictor variables, AICc penalizes model complexity and therefore avoids overfitting (Zeng et al., 2016). Only hinge features, combining linear and step functions, were used (Elith, Kearney, & Phillips, 2010). To test the

transferability of the model, we used a “masked geographically structured” evaluation approach, where the study area was divided into k geographic blocks and evaluation was done on each block in turn (Radosavljevic & Anderson, 2014). Background sampling was performed on all areas apart from the test block to enhance independence of the test data. This was done in R using the ENMeval package (Muscarella et al., 2014), with $k = 4$. For comparison, evaluation results using a less stringent, but commonly applied, approach of bootstrapping over a test percentage of 25% of randomly selected occurrence points are reported. To facilitate model interpretation and the comparison of areas of high, low and no suitability, continuous model outputs were classified using two different thresholds. As a conservative approach, the minimum training presence threshold (MTP) was selected (omission error = zero) in order to identify areas of minimal suitability (Pearson, Raxworthy, Nakamura, & Townsend Peterson, 2007). Additionally, we used the equal sensitivity and specificity (ESS) threshold, where specificity equals sensitivity (the probability of false positives is the same as for false negatives, which is commonly applied to classify habitat suitability (Jiménez-Valverde & Lobo, 2007)) to further classify between low/medium and high suitability habitat. From the Full model, we tested the importance of each of the 30 parameters in predicting grayling distribution, including climate, water chemistry, land cover and predator density data.

2.4 | Testing association of habitat suitability and population inbreeding

To examine associations between habitat suitability and genetic diversity, averages of suitability estimates were taken for all rivers with coverage of at least 40% of the tributary area and where both neutral and adaptive genetic data were available (Rivers Aire, Dee, Derbyshire Derwent, Dove, Eden, Hampshire Avon, Itchen, Severn, Wye and Wylfe; Figure 1). Neutral genetic data of ten microsatellite loci were derived from Dawney, Dawney, Hughes, Cove, and Taylor (2011), and adaptive genetic data for the same populations were derived for the α and β chain of the major histocompatibility (MH) class II from Huml, Taylor, Harris, Sen, and Ellis (2018). Populations were classified according to the mean estimated suitability of the tributary in which they were sampled. Where the mean estimated suitability of the tributary was above the ESS threshold, sites were classified as high suitability habitats. Low suitability habitat was assigned to sites where mean estimated suitability estimates were below the ESS. A Mann–Whitney U test was done to test for significant difference in observed and expected heterozygosity, allelic richness and inbreeding coefficient F_{IS} for both adaptive and neutral markers between high and low suitability habitats (Dawney et al., 2011). A clustered Mann–Whitney–Wilcoxon test implemented in the R package “clusrank,” using 1,000 bootstrap cycles (Jiang, He, Lee, Rosner, & Yan, 2017), was used to account for the dependency of measurements derived from the linked DAA and DAB genes, respectively. The Benjamini–Hochberg method was used to account for multiple testing (Hochberg & Benjamini, 1990). When a

significant relationship between habitat suitability and genetic diversity was identified (see RESULTS), we further tested the relative importance of effective population size (from Dawney et al., 2011) and management background (native non-stocked, native stocked or introduced) on genetic diversity using a Random Forest analysis in the R package randomForest (Liaw & Wiener, 2002).

2.5 | Future distribution under differing climate change scenarios

Data for future climate scenarios were downloaded from the WorldClim database (Hijmans et al., 2005) for the General Circulation Model HadGEM2-AO (UK Meteorological Office, United Kingdom) for each of the representative concentration pathways (RCP) assuming minimal change (RCP 2.6) and maximal change (RCP 8.5) for 2050. Future mean water temperatures in summer were estimated by calculating the percentage degree of change for mean air temperatures in the warmest quarter (Bio 10) under each scenario and applying the same percentage degree of change to current mean water temperatures in summer. It has to be noted that this represents a simplification, as depending on geology (e.g. groundwater influx) and flow regime, water bodies will not always increase linearly with air temperature. Eleven future flow scenarios were obtained from simulations carried out by the Centre for Ecology and Hydrology (CEH) for 2050 (Prudhomme et al., 2013; Prudhomme, Young, et al., 2012). The 11-member ensemble future simulations were generated using the delta change method by running the semi-distributed hydrological model CERF set-up for Great Britain with future scenarios representative of the 2050s based on the UK Met Office Regional Climate Model HadRM3-PPE and compared with a baseline simulation based on observed input from 1961 to 1990 (more details in Prudhomme, Dadson, et al., 2012). The simulations cover a range of different geological river types such as clay, sandstone, limestone and chalk streams, where grayling occur. Uncertainty for future flow simulations was assessed in relation to baseline flow regime (see Prudhomme, Young, et al., 2012). Model inputs and parameters were set as described for the fine-tuned subset model described above. Future projections were made using 100 replicates for each of the eleven future flow scenarios. Standard deviations between flow scenarios were low (see RESULTS), and therefore, predictions were averaged across scenarios. A multivariate environmental similarity matrix (MESS) was created in Maxent (Phillips & Dudík, 2008), as described in Elith et al. (2010), and the variable that is subject to the greatest change in future scenarios was identified.

2.6 | Evaluating the effects of habitat improvement

To evaluate the effect of habitat improvement as a mitigation strategy under climate change conditions, future projections were also

done under scenarios where either orthophosphate, nitrite or copper concentration was artificially manipulated independently or targeting all three parameters in combination. Here, concentrations were capped at the maximum values that had been shown not to impact on habitat suitability estimates for grayling (0.15 mg/L, 0.02 mg/L and 2 µg/L for orthophosphate, nitrite or copper concentration respectively; see RESULTS). These variables were selected, because they were shown to affect habitat suitability for grayling in the Full model (see RESULTS) and could be targeted through management within a habitat improvement context.

3 | RESULTS

3.1 | Comparison of Full and Simple model

The Full model (including non-climatic parameters) showed a better relative performance than the Simple model (which was restricted to just the bioclimatic variables; delta AICc = 4,374). The habitat suitability predicted by the Simple and Full model, respectively, across the study area is shown in Figure 2. The classified predictions of the two models agree in 66% of the study area (Figure 2). In 20% of the study area, the Simple model predicts higher suitability than the Full model, and in 14% of the area, the Simple model predicts lower suitability than the Full model (Figure 2). Tuning of regularization resulted in an optimal random multiplier of 2.2, which represents an increased penalization on model complexity compared to the default value of 1. The Simple model did not show a high performance (mean test AUC across evaluation blocks of 0.71 ± 0.05 (compared to 0.77 ± 0.02 using a bootstrap approach), an average minimum test omission rate of 0.02 ± 0.00007 , and an average 10th percentile omission rate was 0.26 ± 0.04). Twelve out of thirty parameters were retained in the Full model after the variable selection process. This Full model performed better than the Simple model (the average test AUC of the Full model across evaluation blocks was 0.76 ± 0.002 (compared to 0.78 ± 0.02 using a bootstrap approach), which is indicative of a useful model (AUC > 0.75; Elith et al., 2006), an average minimum test omission rate was 0.004 ± 0.00005 , and an average 10th percentile omission rate was 0.12 ± 0.002).

3.2 | Full model

When using the Full model, 11% of the area was classified as unsuitable (below MTP), 61% as low/medium suitability (below ESS) and 28% as high suitability (above ESS; Figure 2). Climatic environmental parameters contributed 51% of the final set of variables used to build the model. These were precipitation of the wettest quarter (Bio 16), isothermality (Bio 3), described as the ratio of the mean diurnal range (Bio 2) to the mean annual range (Bio 7), maximum temperature in the warmest month (Bio 5) and mean water temperature in summer and the 90th (Q10) percentile and 5th (Q95) of annual flow, representing highest and lowest flow

rates, respectively. Water chemistry parameters had a total contribution of 37% to the final model (Table 2). These parameters were the concentrations of calcium, dissolved copper, nitrite and orthophosphates. Further, land cover had a contribution of 12% and cormorant density had a contribution of less than 1% (Table 2). This was also the case using a presence/absence layer of cormorant occurrence observations within 10 km² as an alternative modelling input, which showed minor differences in model predictions (average per cell standard deviation was 0.007).

As a main model output, the sensitivity of grayling to different environmental parameters was quantified. A probability of grayling presence above 50% was observed for (a) maximum temperatures in the warmest month (Bio 5) between 19 and 20.8°C, (b) isothermality values above 36, low flow (Q95) between 1 and just over 5 m³/s, (c) calcium concentrations between ~ 60 and ~ 105 mg/L, (d) orthophosphate concentration between 0.02 and 0.2 mg/L, (e) copper concentrations between 0 and 2.6 µg/L, (f) mean water temperature in summer between 8 and 16°C, (g) precipitation in the wettest quarter between 182 and 306 mm, (h) nitrite concentrations between ~ 0.01 and ~ 0.04 mg/L, (i) high flow (Q10) between 10 and 70 m³/s and (j) no *Phalacrocorax carbo* count within 10 km² (Figure S1). Highest suitability in regard to land use was observed for fruit trees and berry plantations, inland marshes and broadleaf forest. Land use classifications with a probability of presence below 50% were observed for urban fabric and industrial or commercial areas, natural grasslands and moors and heathlands (Figure S1).

3.3 | Association of habitat suitability and population inbreeding

No differences were observed between high and low suitability habitats for observed or expected heterozygosity and allelic richness. Inbreeding coefficients (F_{IS}) were significantly higher in low suitability habitats, defined by the Full model than in high suitability habitats for MH class II markers (clustered Mann–Whitney–Wilcoxon test, $p < .001$) but not for neutral markers (Figure 3). Random Forest analysis also showed high relative importance of habitat suitability estimates compared to effective population size and management background in explaining variation in MH II F_{IS} values (Table 3). Habitat suitability was the parameter that mostly decreased the mean square error (MSE) (Table 3). When using the mean decrease in Gini index as measure of variable importance, both habitat suitability and effective population size were ranked most important (Table 3). No significant differences in genetic diversity were observed between areas of low and high suitability defined by the Simple model.

3.4 | Future projections

Under conditions of climate change, the projections for 2050 predict predominantly a significant loss of high suitability habitat

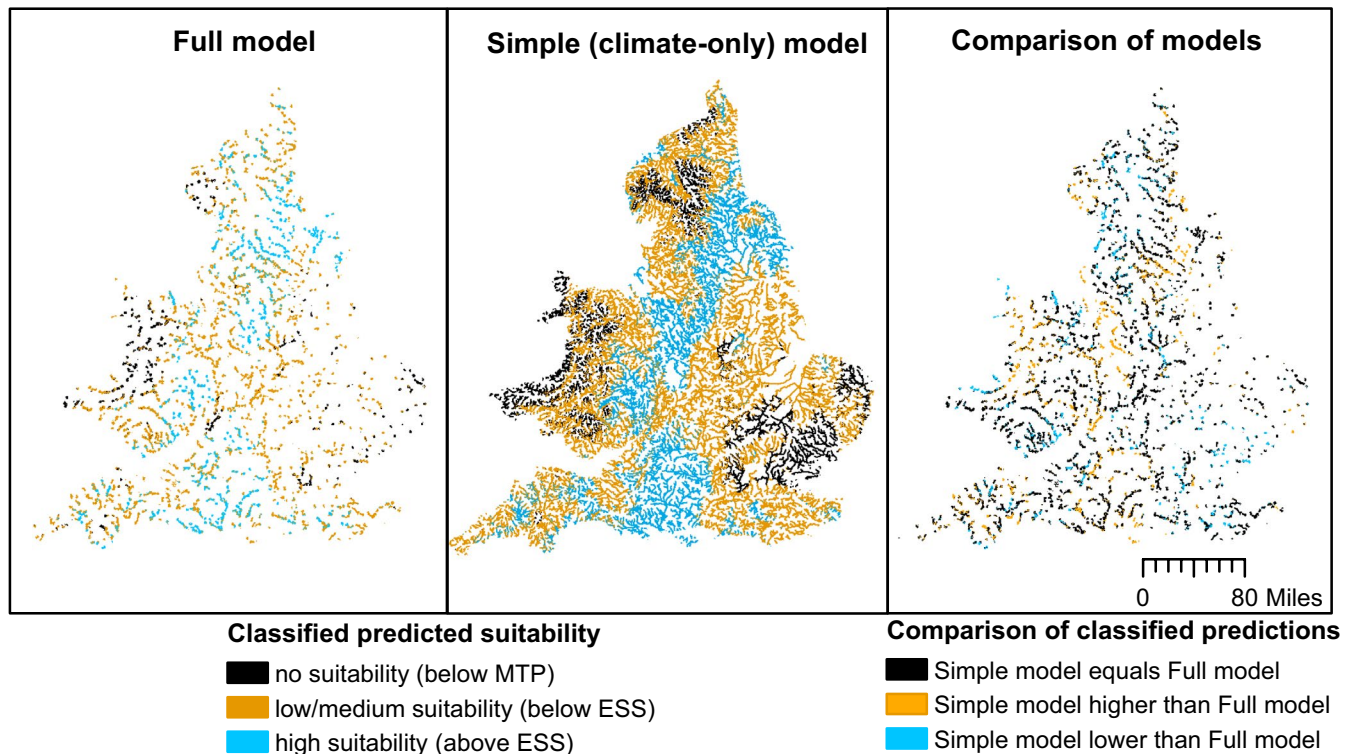


FIGURE 2 Maxent estimates of habitat suitability for *Thymallus thymallus*; Left: Full model; Middle: Simple model; Right: comparison of estimates of the Full and Simple model

TABLE 2 Relative contribution and permutation importance for all variables included in the Full model

| Parameter description | Contribution | Permutation importance |
|--|--------------|------------------------|
| Maximum temperature of the warmest month (Bio 5) | 8.02 | 24.31 |
| Isothermality (Bio 2/ Bio 7) (* 100) (Bio 3) | 10.54 | 15.27 |
| Land cover | 12.06 | 12.83 |
| Low flow (95th quantile of annual flow) | 10.35 | 10.45 |
| Calcium concentration | 20.67 | 9.67 |
| Orthophosphate concentration | 12.15 | 7.95 |
| Dissolved copper concentration | 2.18 | 5.36 |
| Summer mean water temperature | 6.55 | 4.89 |
| Precipitation of the wettest quarter (Bio 16) | 9.10 | 4.14 |
| Nitrite concentration | 2.26 | 2.88 |
| High flow (10th quantile of annual flow) | 5.94 | 1.21 |
| <i>Phalacrocorax carbo</i> density | 0.17 | 1.05 |

Note: Parameters are ranked by permutation importance.

(Figure 4; Table 4). This was estimated as a reduction in highly suitable areas of 21% for the RCP 2.6 and the RCP 8.5 scenario of change (Table 4). Projections for different future flow scenarios were similar, with a maximum per cell standard deviation of 0.033 for the RCP 2.6 and 0.032 for the RCP 8.5 scenario of change. An increase in the area that becomes unsuitable is more pronounced in the RCP 2.6 projection of change, where isothermality (Bio 2/ Bio 7) decreases more, particularly in the South West, due to a

greater increase in the annual temperature range (Bio7) in relation to the diurnal range (Bio2). For the RCP 8.5 projections, the diurnal range increases more proportionally, so that the decrease in isothermality is less pronounced (Figure 4). Large parts of the study area exhibit environmental conditions under climate change scenarios not included in training (Figure S2), which was mainly driven by the increase in maximum temperature of the warmest month (Bio 5).

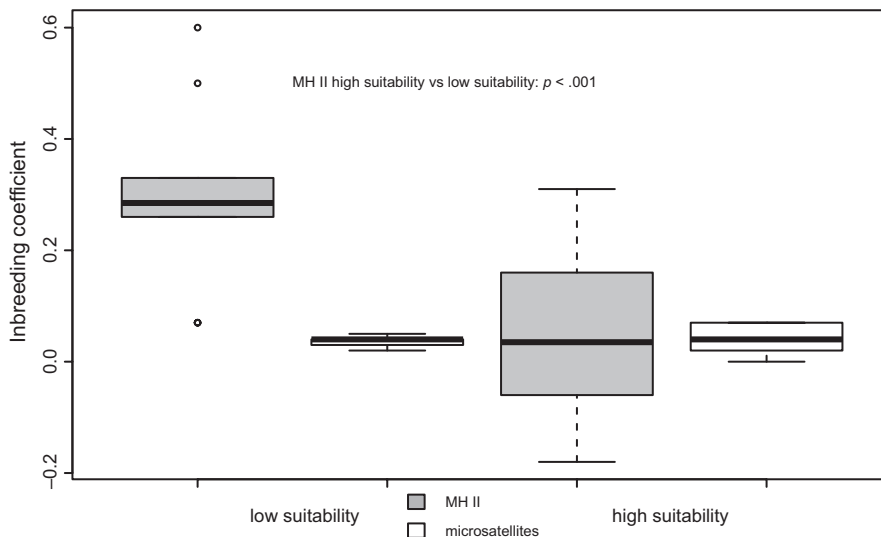


FIGURE 3 Relationship between inbreeding measured for neutral and immune genetic markers and habitat classification: the equal specificity and sensitivity threshold (ESS) is used to classify low and high suitability, respectively

TABLE 3 Random Forest analysis with the MH II inbreeding coefficient F_{IS} as a response variable and habitat suitability (Hs), effective population size (N_e) and management class (class) as predictor variables

| | %IncMSE | IncNodePurity |
|-------|---------|---------------|
| Hs | 13.32 | 0.16 |
| N_e | 8.63 | 0.16 |
| class | 2.93 | 0.12 |

Note: Mean Decrease Accuracy (%IncMSE) and Mean Decrease Gini (IncNodePurity) representing relative variable importance

3.5 | Evaluating the effects of habitat improvement

Decreasing orthophosphate, nitrite or copper concentration in areas where they exceed the estimated tolerance of grayling showed recovery of suitable habitat is possible under current and future conditions (Table 5, Figures 5 and 6). An overall recovery of suitable habitat of up to 7%, 6% and 4% relative to the total study area is predicted to be possible by making locally optimal improvements in either orthophosphate, nitrite or copper concentration under current conditions and predictions for 2050 for the RCP 2.6 and 8.5 scenarios, respectively (Table 5). If the target parameters are optimized in combination, the total improvements of suitability classifications are further increased and estimated 14%, 10% and 6% in total for current and future scenarios (RCP 2.6 and 8.5), respectively (Table 5). Possible improvements would greatly affect areas in which grayling is currently present (Figures 5 and 6). The highest net total gain in estimated suitability that can be achieved reveals locally optimal strategies for improvement, targeting either orthophosphate, nitrite or copper concentration (Figure 6). Highest local increases in habitat suitability of 26% were observed for reductions in orthophosphate concentrations under current conditions (Figure 6). For other locations, a reduction in nitrite or metal pollution had higher effects on suitability achieving relative

maximum improvements of 20% and 17% under current conditions (Figure 6).

4 | DISCUSSION

Here, we modelled habitat suitability for grayling across the UK and we (a) show that distribution models incorporating climate and other habitat parameters outperform climate-only models; (b) present evidence for increased inbreeding coefficients at immune but not neutral markers in areas of low habitat suitability; (c) illustrate significant alterations in range under future climate models; and (d) demonstrate the potential alleviation of range contraction by habitat mitigation.

4.1 | Simple versus Full model

In this study, the Full model including climate and other habitat quality data was much more accurate than the climate-only model (the Simple (climate-only model) showed a 10th percentile omission rate almost twice as high as the Full model). This finding highlights the importance of considering habitat quality parameters that are not explicitly climate related to inform conservation management at local scales. That the inclusion of additional parameters improves models is not surprising as flow has been identified as a critical driver of habitat suitability for freshwater fish (VanCompernelle, Knouft, & Ficklin, 2019) and land use change and pollution have also been implicated in habitat loss or degradation of freshwater habitats (Alabaster & Lloyd, 2013; Foley et al., 2005).

4.2 | Habitat suitability and immune genetic diversity

We found that inbreeding coefficients (F_{IS}) were significantly higher in areas identified as low suitability habitats for adaptive,

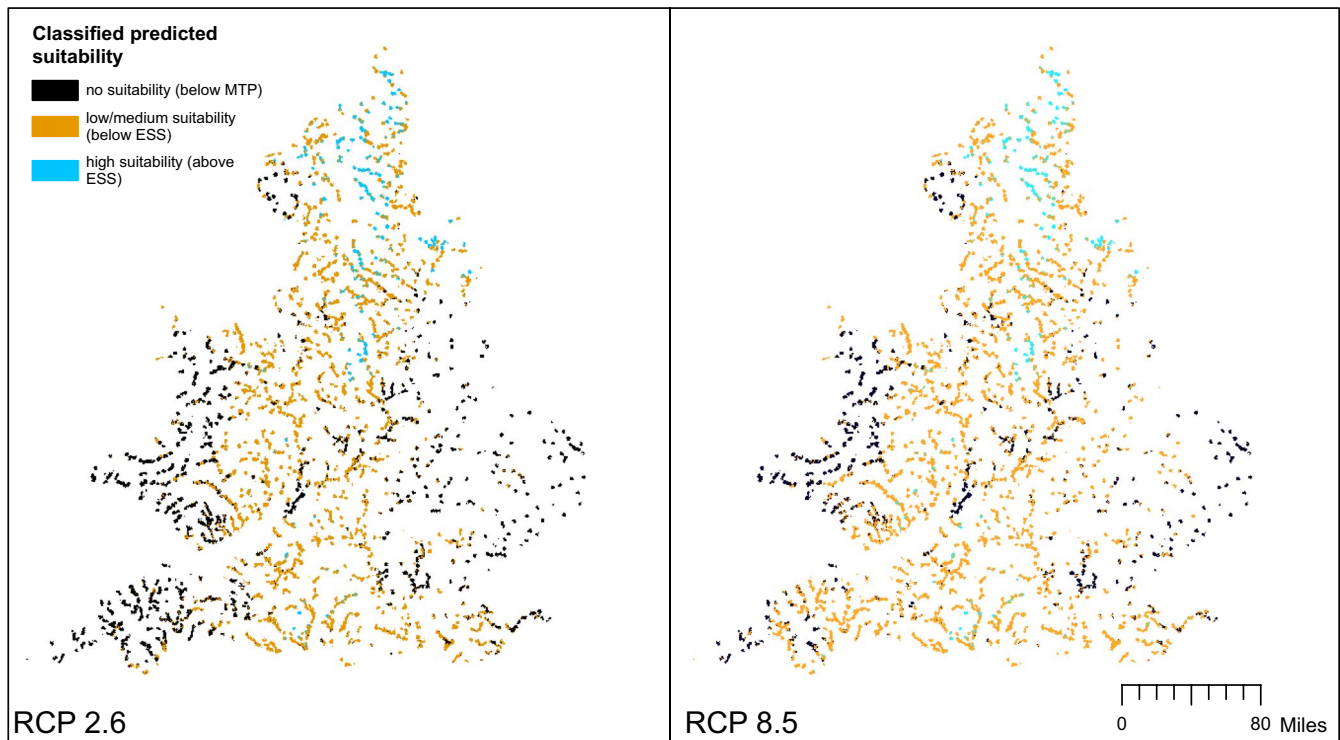


FIGURE 4 Projections of habitat suitability estimates for 2050 for RCP 2.6 (left) and 8.5 (right): Averages across 100 replicates are shown (the mean standard deviation was 0.06 for both the 2.6 scenario and the 8.5 scenario of change across the study area), with warmer colours indicating higher suitability; habitat classifications were done using the minimum training presence threshold (MTP) and equal training sensitivity and specificity (ESS) threshold

TABLE 4 Relative percentage change in habitat classification for 2050

| | current | 2050 RCP 2.6 | 2050 RCP 8.5 |
|------------------------------------|---------|--------------|--------------|
| No suitability (below MTP) | 11 | 35 | 21 |
| Low/medium suitability (below ESS) | 61 | 57 | 73 |
| High suitability (above ESS) | 28 | 7 | 7 |

Note: Relative area in percentage under the following classification: no suitability (below MTP), low/medium suitability (below ESS) or high suitability (above ESS) for the current habitat suitability estimate and as projected for 2050 under the RCP 2.6 and 8.5, respectively

immune system markers. This was not the case for neutral markers. Biased sampling of kin or the Wahlund effect (Wahlund, 1928) is unlikely to explain this result, as both types of markers would be equally affected. Inbreeding caused by a recent population decline or higher variation in family size as a consequence of the reduced habitat quality would also be expected to be reflected by neutral markers. A technical artefact, such as a higher probability for the presence of null alleles at the MH II in samples from low suitability habitats, seems unlikely, as samples were prepared in duplicates

and random order (see Huml et al., 2018). Taking other potential drivers, such as effective population size and management background into account in the Random Forest analysis, habitat quality best explains the observed patterns of F_{IS} at immune genes. There is evidence that the prevalence of infectious disease and the susceptibility of hosts can be increased under unfavourable environmental conditions (Austin, 2007; Schmidt-Posthaus & Wahli, 2015). This includes metal pollution and eutrophication (Shirakashi & El-Matbouli, 2010; Wedekind, Gessner, Vazquez, Maerki, & Steiner, 2010), which were also identified to be among the main factors impacting on habitat suitability for grayling in this study. While our small sample size ($N = 10$) demands cautious interpretation of our results, we suggest directional selection pressure on MH II genes as a plausible explanation. This could be due to a higher prevalence of opportunistic pathogens under conditions of reduced habitat quality or environmental stress (Austin, 2007; Boutin, Bernatchez, Audet, & Derôme, 2013; Schmidt-Posthaus & Wahli, 2015), resulting in significantly higher F_{IS} observed at the MH II for low-quality habitats, but with no observed effect of habitat quality for microsatellites. This is of high conservation relevance as periods of increased pressures of disease-mediated directional selection can lead to significant losses of immune genetic diversity and the future potential to face pathogens (Coughlan et al., 2006). However, a direct measure of selection pressures, for example through the assessment of shifts in the microbiome composition in grayling in

| | Orthophosphate (0.15 mg/L) | Nitrite (0.02 mg/L) | Copper (2 µg/L) | All combined |
|-----------------------|-------------------------------|------------------------|-----------------|--------------|
| Current | | | | |
| Increase above MTP | 2 | 2 | 2 | 3 |
| Increase above ESS | 3 | 3 | 5 | 11 |
| RCP 2.6 | | | | |
| Increase above MTP | 4 | 4 | 5 | 9 |
| Increase above ESS | 0.5 | 1 | 1 | 1 |
| RCP 8.5 | | | | |
| Increase above MTP | 3 | 2 | 3 | 5 |
| Increase above ESS | 1 | 1 | 1 | 1 |

TABLE 5 Relative percentage change in habitat classification for 2050, when orthophosphate, nitrite or copper concentration is reduced to the maximum estimated as tolerable

Note: Relative increase in suitable area in percentage under the following classification: no suitability (below MTP), low/medium suitability (below ESS) or high suitability (above ESS) as projected for current conditions and for 2050 under the RCP 2.6 and 8.5, respectively, when either orthophosphate, nitrite or copper concentration is reduced independently or when all three parameters are reduced in combination.

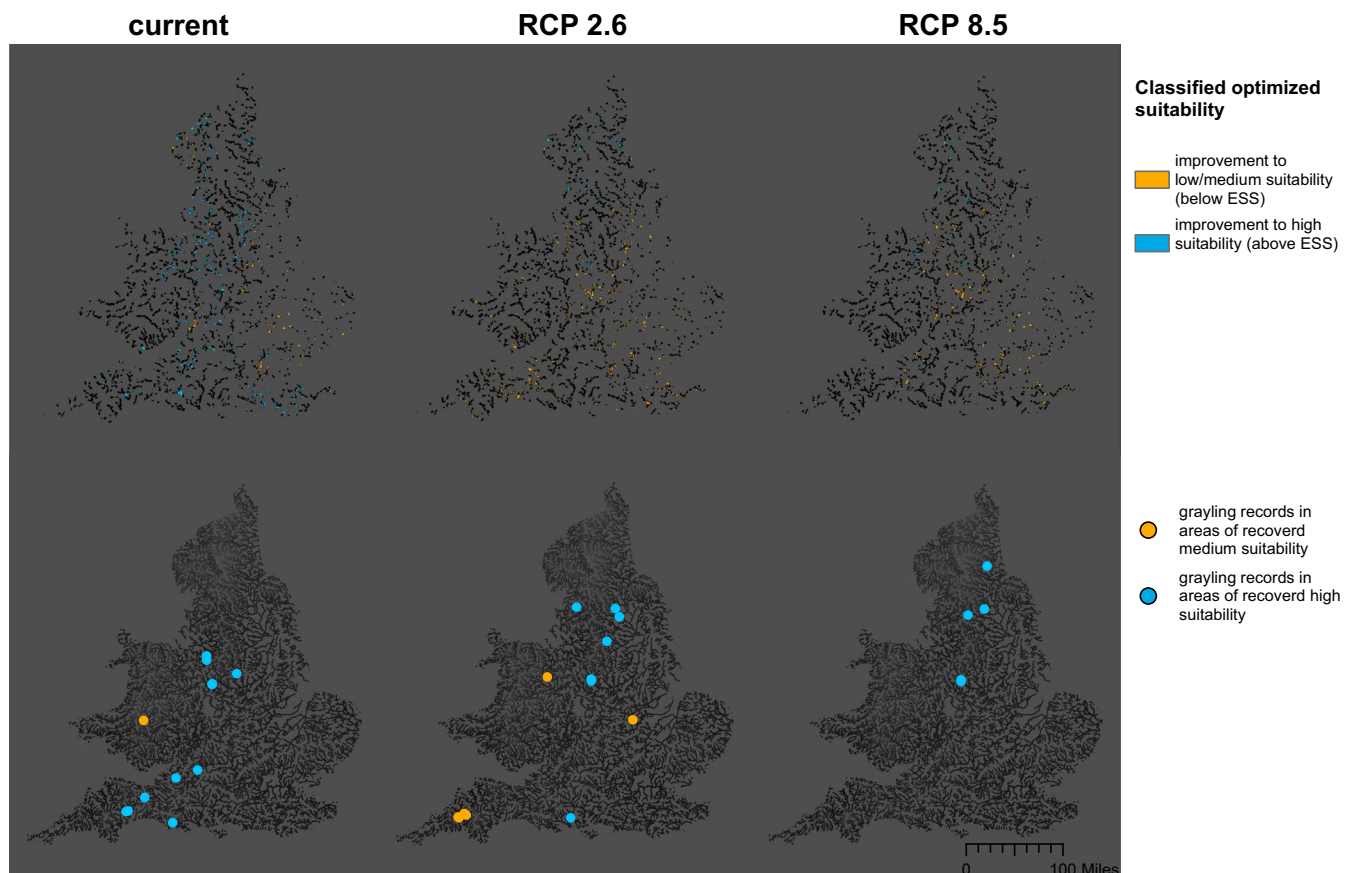


FIGURE 5 Classified predictions of habitat suitability estimates for current conditions and 2050 for RCP 2.6 and 8.5 when locally orthophosphate, nitrite and copper are reduced to maximum values estimated not to affect habitat suitability for grayling: top panels: increase in classified suitability observed across the study area; bottom panels: sites with current occurrences of grayling that are positively affected by reducing either orthophosphate, nitrite or copper concentrations

relation to their MH genotype within low-quality habitats, would be required to confirm this hypothesis.

4.3 | Future climate predictions

Significant reductions in suitable range for grayling under future climate predictions were also demonstrated. As climate change occurs, species will need to respond either adaptively or by tracking range changes (Hoffmann & Sgro, 2011). That there is a scope for adaptive responses to climate change in salmonids has been shown by several studies. Eliason et al. (2011) showed that populations of sockeye salmon (*Onchorhynchus nerka*) exhibit different tolerance limits to temperatures, reflecting historic temperature ranges of their habitat. An adaptive population divergence in response to temperature has been shown by Kavanagh, Haugen, Gregersen, Jernvall, and Vøllestad (2010) arising quickly and under constraining conditions of continued gene flow and previous bottlenecks in grayling. Jensen et al. (2008) showed significant differences in

the amount of heritable variation in phenotypic plasticity between populations in response to temperature regimes in brown trout (*Salmo trutta*). Increasing flexibility is thought to be particularly important in response to climate change as environmental conditions are predicted to fluctuate more. The high importance of isothermality in the habitat suitability model for grayling within the UK might indicate that there are selection pressures on increased flexibility present.

Maximum summer temperature was the parameter subject to most change under future projections (Figure S2). While air temperatures generally show a linear relationship to water temperatures, the latter are also affected by flow, water volume, shading and wind shelters and deviations from linearity have been particularly shown, when maximum air temperatures exceed 25°C (Erickson & Stefan, 2000; Webb, Clack, & Walling, 2003). This was also evident from the river surface water temperature data set used here (Orr et al., 2010). Differences in the effect of maximum air temperatures on mean water temperatures may reflect local differences in buffering capacity of the water body. Local thermal

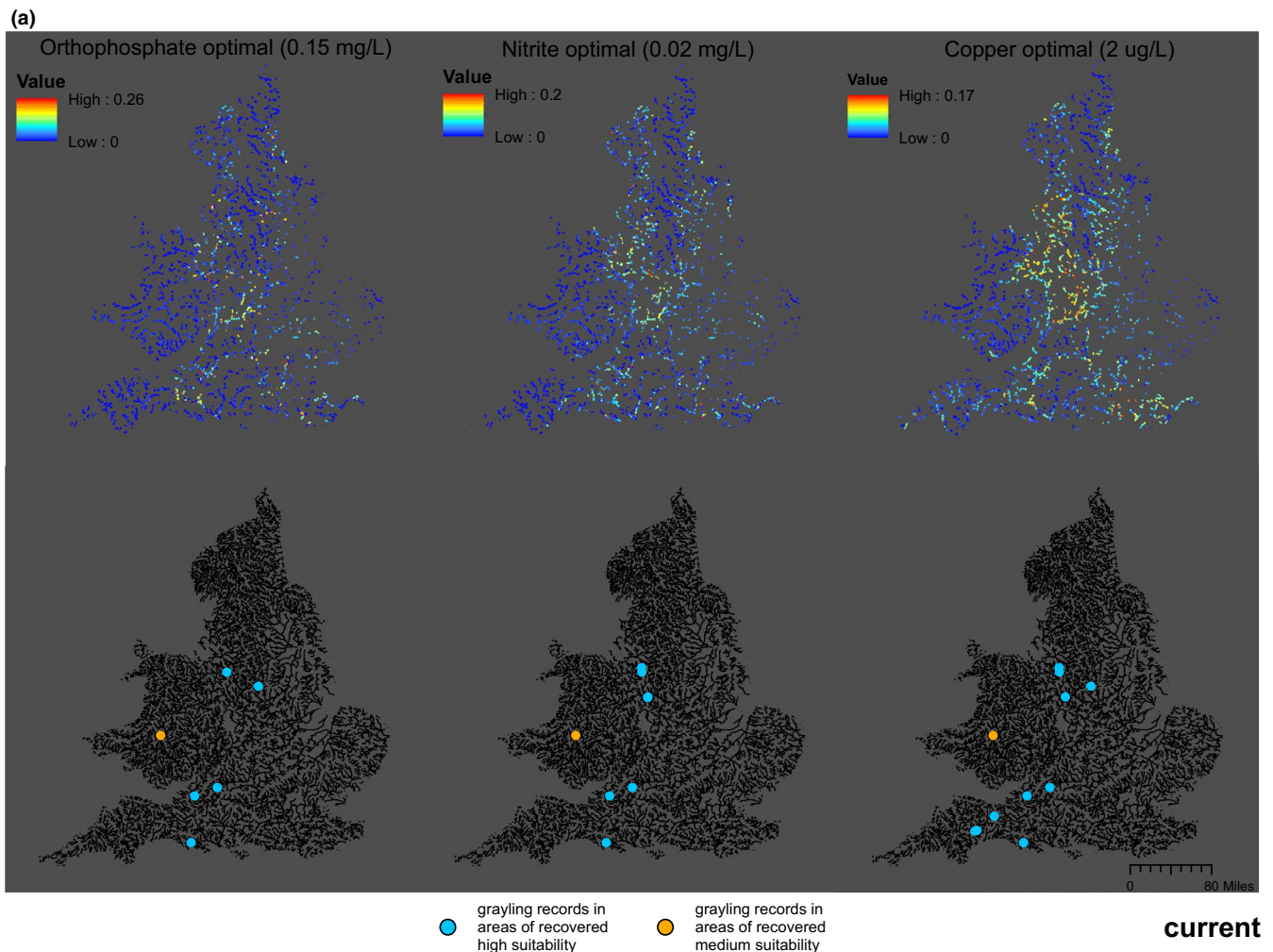


FIGURE 6 Projections of change in habitat suitability estimates for (a) current conditions or 2050 for (b) RCP 2.6 and (c) RCP 8.5 when reducing orthophosphate, nitrite or copper concentrations to maximum values estimated not to affect habitat suitability for grayling: top panels: increase in suitability observed across the study area; bottom panels: sites with current occurrences of grayling that are positively affected by reducing either orthophosphate, nitrite or copper concentrations

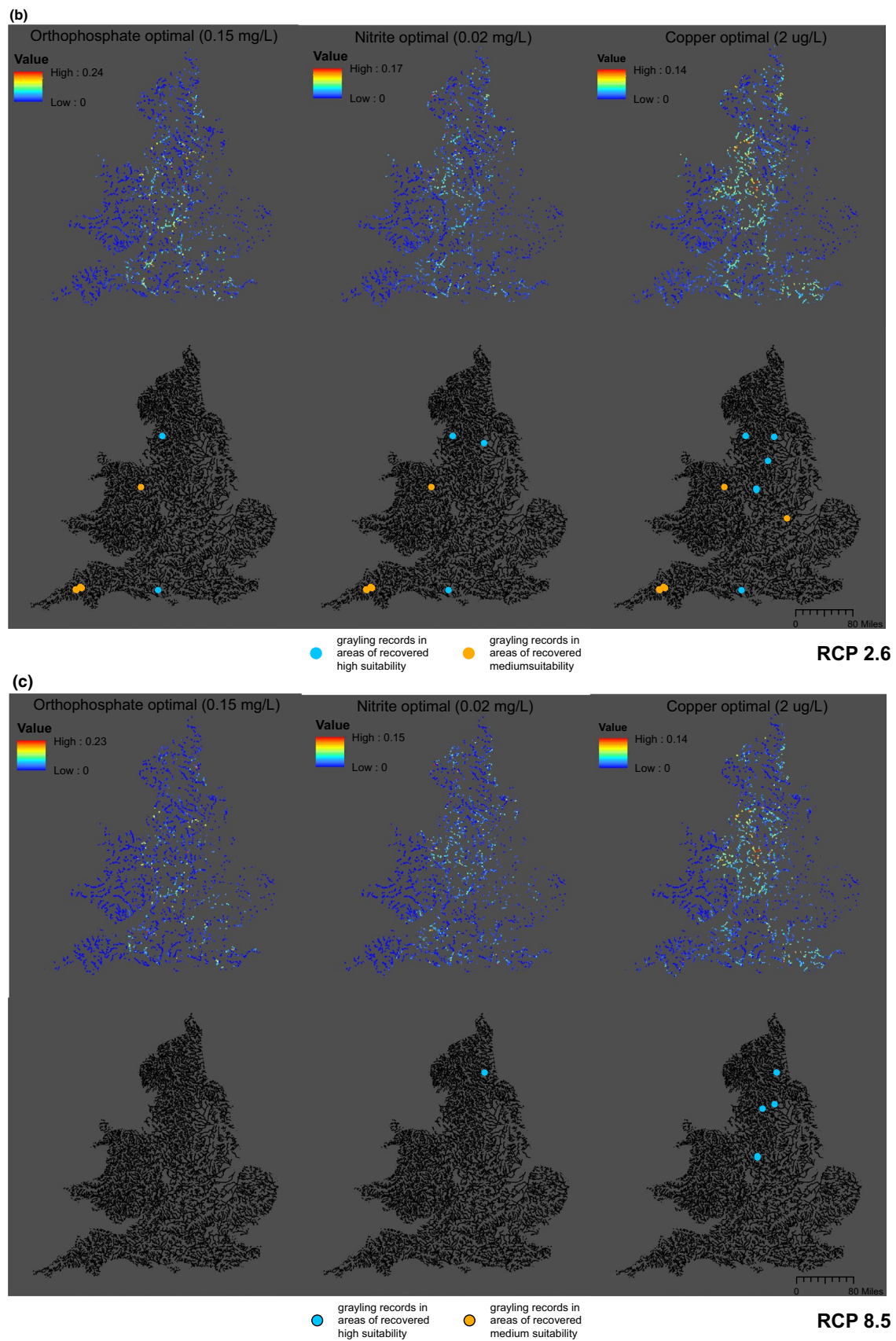


FIGURE 6 Continued

refugia have been shown to be actively used by juvenile salmonids and are potentially important for their survival in a warming climate (Sutton & Soto, 2012). Further investigations on local thermal refugia within grayling rivers that are expected to suffer from temperature increases, such as those in the South East, and management actions, such as the creation of riparian woodland zones are recommended (Malcolm et al., 2008). Also, the effect of groundwater abstraction should be evaluated in this context and in regard to increasing the risk of low summer flows, which can be critical for grayling (Riley et al., 2009).

4.4 | Mitigation of climate change impacts

One of the most important messages of this study is that the models demonstrate that adjustments in environmental parameters maintain habitat suitability under climate change. It is therefore clear that modelling of future distributions should take both climate and non-climate-related parameters into account. Particular environmental parameters of importance (for mitigating range changes) included orthophosphates, nitrites and metal pollution. Organic pollution and eutrophication associated with high concentrations of phosphate and nitrate are one of the major anthropogenic impacts on freshwater systems (Birk et al., 2012; Blabolil et al., 2016). Harmful effects for fish are caused by oxygen depletion, resulting from increased phytoplankton growth (Elshout, Dionisio Pires, Leuven, Wendelaar Bonga, & Hendriks, 2013). Because of temperature dependencies, the impact of eutrophication is expected to further increase under climate change conditions (Moss et al., 2011). Metals have toxic effects on fish, mainly caused by a disruption of mechanisms important for ion regulation (Alsop & Wood, 2011). Metal pollution is considered a serious threat to freshwater ecosystems (Förstner & Wittmann, 2012) and is associated with historic mining activities within the UK (Macklin, Hudson-Edwards, & Dawson, 1997).

5 | CONCLUSIONS

Reducing non-climate-related environmental stress has been highlighted to be among the most important management action in the face of climate change (Heller & Zavaleta, 2009). This is stressed by the findings on low habitat suitability impacting on adaptive genetic variation and likely evolutionary potential, which is thought to be capable to promote climate change adaptation in salmonids (Eliaison et al., 2011).

While this study does not try to give accurate predictions of the future distribution of grayling, its main goal was to show the potential of different habitat improvement strategies to increase habitat suitability for grayling under conditions of climate change and to give specific suggestions on local priority actions. One caveat of our study is that we used Maxent as a single modelling approach. While Maxent generally performs well in comparison with other techniques

(Aguirre-Gutiérrez et al., 2013), the choice of modelling technique has been identified as a major source of uncertainty in SDMs (Thuiller, Guéguen, Renaud, Karger, & Zimmermann, 2019). Therefore, an ensemble SDM approach, which combines several techniques, may be a better alternative to comprehensively quantify uncertainty of predictions (Thuiller et al., 2019). Further, while in this study we successfully identify a number of non-climatic parameters that can be targeted to mitigate negative effects of climate change, we did not exhaustively evaluate all variables that may impact on habitat suitability of grayling. For example, here we focussed on extreme conditions of river flow (Q10 and Q95), given their particular relevance for the survival of juvenile salmonids (Riley et al., 2009; Warren et al., 2015). However, seasonal patterns and variation in the flow regime, as well as the relevance of groundwater influxes, may be another important aspect to consider in future studies. Also, habitat fragmentation through hydropower development and dam construction has been shown to adversely affect grayling populations and maintenance of population connectivity is considered another important conservation priority (Junge, Museth, Hindar, Kraabøl, & Vøllestad, 2014).

Effective conservation of grayling across the higher latitudinal range of the species distribution, such as the UK and Scandinavia, is particularly warranted to safeguard the species, as the effects of climate change are expected to be less drastic than across its lower latitudinal range. The importance of evaluating priorities and invoking management actions on habitat improvement within the continental distribution of grayling is clear, given an expected stronger effect of climate change on habitat suitability for grayling at lower latitudes. In summary, in the UK rivers should be managed to reduce levels of orthophosphates, copper and nitrate to ensure the best prospects for grayling under a changing climate. Evaluation of non-climate parameters should become routine in species distribution modelling for conservation management in a climate change context.

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DATA AVAILABILITY STATEMENT

Occurrence data used in this study and an R-script used to fine-tune model parameters are available on Dryad (<https://doi.org/10.5061/dryad.msbcc2ftz>). All other data used are available publicly or upon request from the sources given in the manuscript.

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BIOSKETCH

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Author contributions: J.V.H. gathered the data and did the modelling and analysis. C.P. contributed current and future flow simulation data. J.V.H. and J.S.E. wrote the manuscript. All authors were involved in informing the study design and editing of the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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